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STRUCTURAL CHANGES ASSOCIATED WITH FACTOR MUTATIONS AND WITH CHROMOSOME MUTATIONS IN DATURA [1]

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The fact has recently been emphasized[2] that two distinct types of mutation may occur in plants—those which are due to the change of a single factor or gene and those which are due to the addition of one or more entire chromosomes. The Jimson Weed, *Datura Stramonium*, displays both of these mutation types. If we consider the purple-flowered, spiny fruited, many-noded form the primitive type, three "factor" mutations have occurred, giving rise to white-flowered, smooth-fruited, and few-noded types; and twelve distinct "chromosome" mutations have been identified and named, each of which has been found to be associated with the addition of an extra chromosome to a particular one of the twelve pairs. Tetraploid plants and other chromosomal aberrations have also been found.

These mutations have been identified by various external characters. The purpose of the present investigation (of which this paper is a preliminary report) is to study and compare the *structure* of these mutant forms, both as to gross external morphology and as to internal anatomy; and thus to determine the structural effects produced by a single factor and those produced by a single entire chromosome. In this way it may be possible to begin an analysis of the factorial constitution of each of the chromosomes.

Externally, various measurements of the gross structure of the plant body were made. Branching in the Jimson Weed is essentially dichotomous and the two branches are usually of decidedly different lengths. These measurements were of (1) the trunk length (height of stalk to the first fork; (2) the width of the angle formed by the branches at the first

fork of the stem; (3) the width of the angles formed by the branches at the two second forks; (4) the width of the angles formed by the branches at the four third forks; (5) the length of the internodes forming the first fork; (6) the lengths of the two pairs of internodes forming the two second forks; (7) the lengths of ten of the younger internodes (all of the same age) near the ends of the branches; (8) the diameter of these ten internodes; and (9) the ratio between the length of the two branches above each of these ten internodes. In each type studied, a considerable number of plants were measured and the measurements averaged.

The various factor mutations were compared with the normal type (purple-flowered, spiny-fruited and many-noded). The white-flowered mutant was not found to differ appreciably from the normal type. The smooth-fruited form, however, has significantly narrower angles, shorter internodes, greater stem diameter and greater difference between the two branches at a fork than does the spiny-fruited one; and the few-noded type has a significantly shorter trunk, shorter internodes, narrower stem diameter and greater difference between the two branches at a fork than does the many-noded form. These constitute excellent examples of the manifold effects of a single factor upon the plant body as a whole.

Internally, few constant and characteristic differences between these mutant types and the normal form have as yet been distinguished, but in view of the notable differences in external structure it seems likely that a more complete and detailed anatomical study may reveal such differences.

An investigation was made of the gross external structure of several of the chromosome mutants with a single extra chromosome and each was found to display characteristic and significant differences from the normal type. Compared with the normal, "Reduced," for instance, shows a significant decrease in trunk length, angle width and stem diameter; "Cockleburr" an increase in angle width and a decrease in stem diameter and in internode length; "Globe" a decrease in internode length and an increase in stem diameter and in the difference in length between the two branches at a fork, and "Buckling" an increase in angle width.

Furthermore, a number of these chromosome mutants differ radically from the normal type in their internal structure. Both "Poinsettia" and "Wiry," for example, tend to have an asymmetrical central cylinder, and opposite the thin portions of the cylinder the cortex breaks open and produces a characteristic lesion. In these mutants wedges of wood also extend for some distance into the pith. In both "Cockleburr" and "Wedge," vessels are much more abundant than in the normal type and show a great variation in size. "Reduced" has a well-developed ring of sclerenchyma at the outer edge of the pith and the inner edge of the cortex. "Globe" tends to have thick-walled vessels, very round in cross section.

In "Buckling" the woody cells are very weakly lignified. Other distinctions will doubtless reveal themselves on a more intensive study.

Tetraploid plants from two distinct races were examined. Both showed an elongation of the trunk and an increase in the width of the first angle, the first pair of internodes and the stem diameter. Internally, the cells were found to be significantly larger than in the normal type and the woody tissue tended to be less strongly lignified.

Only a preliminary survey of the field has as yet been made. The authors believe, however, that these Datura cultures provide exceptionally promising material for a study of the effect of specific factors and of specific chromosomes, particularly upon structural characters; and they hope through further investigation to be able to contribute materially to a factorial analysis of the chromosomes of this species.

[1] Paper presented before the Botanical Society of America, December 28, 1921.

[2] Albert F. Blakeslee, "Types of Mutations and Their Possible Significance in Evolution," *Amer. Naturalist*, **55**, 1921 (254–267); and "Variations in Datura Due to Changes in Chromosome Number," *Ibid.*, Jan.–July, 1922.

THE RIEMANN GEOMETRY AND ITS GENERALIZATION

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1. One of the simplest ways of generalizing Euclidean Geometry is to start by assuming (1) that the space to be considered is an n-dimensional manifold in the sense of Analysis Situs, and (2) that in this space there exists a system of curves called *paths* which, like the straight lines in a euclidean space, serve as a means of finding one's way about.

These paths are defined as the solutions of a system of differential equations,

$$\frac{d^2x^i}{ds^2} + \Gamma^i_{jk}\frac{dx^j}{ds}\frac{dx^k}{ds} = 0, \qquad (1.1)$$

in which the Γ^i_{jk}'s are analytic functions of $(x^1, x^2, \ldots, x^n)$ and the indices i, j, k run from 1 to n. The second term is a summation with regard to j and k in accordance with the usual convention in such formulas that any term represents a summation with respect to each letter which appears in it both as a subscript and as a superscript.

Since the second term is a quadratic form in $\frac{dx^i}{ds}$, there is no loss of generality in assuming, as we do, that

$$\Gamma^i_{jk} = \Gamma^i_{kj} \qquad (1.2)$$

This definition of the *paths* is immediately suggested by the fact that the differential equations of the straight lines in a euclidean space which are

$$\frac{d^2x^i}{ds^2}=0 \tag{1.3}$$

in cartesian coördinates, take the form (1.1) in general coördinates, the Γ's now being such that there shall exist an analytic transformation of $(x_1, x_2, \ldots x_n)$ converting (1.1) into (1.3).

2. This generalized geometry has been studied by H. Weyl in his book, "Raum, Zeit, Materie," Berlin, 1919, and in Vol. 1 of the "Mathematische Zeitschrift." It has also been considered by A. S. Eddington in *Proc. Roy. Soc. London*, **99A** (1921). Both these authors define it in terms of a generalization of Levi-Civita's concept of infinitesimal parallelism rather than by the more natural idea of a system of paths.

It reduces to the Riemann geometry if we assume that there exists a quadratic form

$$g_{ij}\frac{dx^i}{ds}\frac{dx^j}{ds} \qquad (g_{ij}=g_{ji}) \tag{2.1}$$

with respect to which the paths are geodesics, i.e., if the curves for which the integral

$$\int \sqrt{g_{ij}\frac{dx^i}{ds}\frac{dx^j}{ds}}\,ds \tag{2.2}$$

is stationary satisfy the differential equations (1.1). The conditions that (2.2) be stationary are

$$g_{\alpha i}\Gamma^{\alpha}_{jk}=\frac{1}{2}\left(\frac{\partial g_{ji}}{\partial x^k}+\frac{\partial g_{ki}}{\partial x_j}-\frac{\partial g_{jk}}{\partial x^i}\right). \tag{2.3}$$

When solved for the derivatives of the g's these conditions become

$$\frac{\partial g_{ij}}{\partial x^k}-g_{\alpha j}\Gamma^{\alpha}_{ik}-g_{i\alpha}\Gamma^{\alpha}_{jk}=0. \tag{2.4}$$

3. In general there exists no quadratic form (2.1) for which the paths are geodesics. For example, in a two-dimensional manifold the system of paths defined by

$$\begin{aligned}\frac{d^2x^1}{ds^2}+(x^1-x^2)\left(\frac{dx^1}{ds}\right)^2&=0,\\ \frac{d^2x^2}{ds^2}+(x^1-x^2)\left(\frac{dx^2}{ds}\right)^2&=0\end{aligned} \tag{3.1}$$

is one for which the equations (2.4) are inconsistent. Therefore there exists no quadratic form (2.1) of which the paths (3.1) are geodesics.

The problem of determining under what conditions the geometry of

paths is Riemannian is one of the inverse problems of the Calculus of Variations. But it does not seem hitherto to have been solved. Before considering it further we must mention a few general theorems, which have already been noted more or less explicitly by Weyl and Eddington.

4. If we put $x^i = \varphi^i(\bar{x}^1, \ldots \bar{x}^n)$, thus introducing a new set of coördinates, the equations (1.1) become

$$\frac{d^2\bar{x}^i}{ds^2} + \bar{\Gamma}^i_{jk}\frac{d\bar{x}^j}{ds}\frac{d\bar{x}^k}{ds} = 0, \tag{4.1}$$

where

$$\frac{\partial^2 x^p}{\partial \bar{x}^i \partial \bar{x}^j} + \Gamma^p_{qr}\frac{\partial x^q}{\partial \bar{x}^i}\frac{\partial x^r}{\partial \bar{x}^j} = \bar{\Gamma}^i_{ij}\frac{\partial x^p}{\partial \bar{x}^i}. \tag{4.2}$$

Expressing the conditions of integrability of these equations regarded as differential equations for determining the x's as functions of the $\bar{x}$'s, when the Γ's and $\bar{\Gamma}$'s are known, we obtain

$$\frac{\partial x^q}{\partial \bar{x}^i}\frac{\partial x^r}{\partial \bar{x}^j}\frac{\partial x^s}{\partial \bar{x}^k}B^p_{qrs} = \frac{\partial x^p}{\partial \bar{x}^l}\bar{B}^l_{ijk} \tag{4.3}$$

where

$$B^p_{qrs} = \frac{\partial \Gamma^p_{qs}}{\partial x^r} - \frac{\partial \Gamma^p_{qr}}{\partial x^s} + \Gamma^p_{ar}\Gamma^a_{qs} - \Gamma^p_{as}\Gamma^a_{qr}. \tag{4.4}$$

Equation (4.3) may also be written

$$\frac{\partial x^q}{\partial \bar{x}^i}\frac{\partial x^r}{\partial \bar{x}^j}\frac{\partial x^s}{\partial \bar{x}^k}\frac{\partial \bar{x}^l}{\partial x^p}B^p_{qrs} = \bar{B}^l_{ijk}. \tag{4.5}$$

This states that the functions $\bar{B}$ are the components in the coördinate system $\bar{x}$ of a tensor, B, which is contravariant of the first order and covariant of the third order, with respect to the group of all transformations of the paths into themselves. This tensor is called the *curvature tensor* of the manifold.

From (4.4) it follows that

$$B^p_{qrs} + B^p_{qsr} = 0, \tag{4.6}$$

and

$$B^p_{qrs} + B^p_{rsq} + B^p_{sqr} = 0. \tag{4.7}$$

The theory of covariant differentiation (cf. Ricci and Levi-Civita in *Math. Ann.*, **54** (1901)) can be generalized at once to the geometry of paths by replacing the Christoffel symbols $\left\{\begin{matrix} jk \\ i \end{matrix}\right\}$ by the functions Γ^i_{jk} in all formulas. In particular it is easily proved by means of (4.1) and (4.2) that the operation of covariant differentiation converts any tensor into a tensor of higher order. The formulas for covariant differentiation of sums and products of tensors also generalize without change, and also the theorem that if a_{ij} is any tensor and a_{ijkl} is its second covariant derivative,

$$a_{ijkl} - a_{ijlk} = a_{aj}B^a_{ikl} + a_{ia}B^a_{jkl}. \tag{4.8}$$

5. Returning now to the question as to the conditions on the Γ's that they shall yield a Riemann geometry, we observe that the left hand member of (2.4) is the covariant derivative of g_{ij}. Thus (2.4) may be written

$$g_{ijk} = 0. \tag{5.1}$$

By (4.8)

$$g_{ijkl} - g_{ijlk} = g_{\alpha j} B^{\alpha}_{ikl} + g_{i\alpha} B^{\alpha}_{jkl} \tag{5.2}$$

which combined with (5.1) gives

$$g_{\alpha j} B^{\alpha}_{ikl} + g_{i\alpha} B^{\alpha}_{jkl} = 0. \tag{5.3}$$

If these equations be differentiated covariantly, we get

$$g_{i\alpha} B^{\alpha}_{jklm} + g_{\alpha j} B^{\alpha}_{iklm} + g_{i\alpha m} B^{\alpha}_{jkl} + g_{\alpha jm} B^{\alpha}_{ikl} = 0. \tag{5.4}$$

Hence by (5.1)

$$g_{i\alpha} B^{\alpha}_{jklm} + g_{\alpha j} B^{\alpha}_{iklm} = 0. \tag{5.5}$$

Proceeding in this manner we get a sequence of equations, namely

$$\begin{gathered} g_{i\alpha} B^{\alpha}_{jklmn} + g_{\alpha j} B^{\alpha}_{iklmn} = 0, \\ \cdots\cdots\cdots\cdots\cdots\cdots \\ g_{i\alpha} B^{\alpha}_{jklmn \cdots p} + g_{\alpha j} B^{\alpha}_{iklmn \cdots p} = 0. \end{gathered} \tag{5.6}$$

If the geometry of paths is Riemannian (5.1) must be satisfied and hence also (5.3), (5.5) and (5.6). The equations (5.3), (5.5) and (5.6) are linear equations in the $(n+1)n/2$ functions g_{ij} with coefficients which are functions of the Γ's alone. Hence the algebraic conditions for the consistency of (5.3), (5.5) and (5.6) regarded as linear equations in the g's are necessary conditions on the Γ's that the geometry of paths shall be Riemannian.

6. Now suppose that equations (5.3) and (5.5) are algebraically consistent in the g's, and that the rank of the matrix of the B's is such that the g's are determined by (5.3) to within a factor, which is at most a function of the x's. Let g_{ij} stand for a particular solution of (5.3) and (5.5). If (5.3) be differential covariantly with respect to x_m, we have in consequence of (5.5)

$$g_{i\alpha m} B^{\alpha}_{jkl} + g_{\alpha jm} B^{\alpha}_{ikl} = 0. \tag{6.1}$$

Since these equations are of the same form as (5.3), it follows from the above hypothesis about (5.3) that

$$g_{ijk} = \varphi_k g_{ij}, \tag{6.2}$$

where φ_k is a covariant vector. Substituting these expressions in

$$g_{ijkl} - g_{ijlk} = 0, \tag{6.3}$$

which follows from (5.2) and (5.3), we obtain

$$\frac{\partial \varphi_l}{\partial x^k} = \frac{\partial \varphi_k}{\partial x^l}.$$

Hence the vector φ_k is the gradient of a scalar function, and can be put in the form

$$\varphi_k = -\frac{\partial \log \lambda}{\partial x^k}. \tag{6.4}$$

Substituting this value of φ_k in the right member of (6.2) and the explicit expression for g_{ijk} (cf. 2.4) in the left member, we obtain

$$\frac{\partial}{\partial x^k}(\lambda g_{ij}) - \lambda g_{pi}\Gamma^p_{jk} - \lambda g_{pj}\Gamma^p_{ik} = 0. \tag{6.5}$$

Consequently the functions λg_{ij} satisfy (2.4) and give a Riemann geometry.

It is interesting to note that the geometry of paths obtained from (6.2) without imposing the condition (6.4) is the geometry used by Weyl as the basis for a combined electromagnetic and gravitational theory. For (6.2) is equivalent to

$$g_{ak}\Gamma^a_{ij} = \frac{1}{2}\left(\frac{\partial g_{ik}}{\partial x^j} + \frac{\partial g_{jk}}{\partial x^i} - \frac{\partial g_{ij}}{\partial x^k}\right) + \frac{1}{2}(g_{ik}\varphi_j + g_{jk}\varphi_i - g_{ij}\varphi_k). \tag{6.6}$$

7. Let us now assume that (5.3) are algebraically consistent, and that all of their solutions satisfy (5.5). Let $g^{(1)}_{ij}, g^{(2)}_{ij} \ldots\ldots g^{(p)}_{ij}$ be a complete set of solutions. The general solution is expressible in the form

$$g_{ij} = \varphi^{(1)} g^{(1)}_{ij} + \varphi^{(2)} g^{(2)}_{ij} + \ldots. + \varphi^{(p)} g^{(p)}_{ij}. \tag{7.1}$$

Differentiating (5.3) covariantly, we get (6.1), and consequently we must have

$$g^{(\alpha)}_{ijk} = \lambda^{(\alpha 1)}_k g^{(1)}_{ij} + \ldots. + \lambda^{(\alpha p)}_k g^{(p)}_{ij}. \tag{7.2}$$

The p^2 vectors $\lambda^{(\alpha\beta)}_k$ ($\alpha, \beta = 1, \ldots. p$) must be such that the functions $g^{(\alpha)}_{ijk}$ satisfy (6.3). On substituting (7.2) in (6.3) we find

$$\frac{\partial \lambda^{(\alpha\beta)}_k}{\partial x^j} - \frac{\partial \lambda^{(\alpha\beta)}_j}{\partial x^k} + \sum_{\gamma=1}^{p}\left(\lambda_k{}^{(\alpha\gamma)}\lambda_l{}^{(\gamma\beta)} - \lambda_l{}^{(\alpha\gamma)}\lambda_k{}^{(\gamma\beta)}\right) = 0. \tag{7.3}$$

When we express the condition that the functions g_{ij} given by (7.1) shall satisfy the conditions $g_{ijk} = 0$, we find in consequence of (7.2) that the functions $\varphi^{(\alpha)}$ must satisfy the equations

$$\frac{\partial \varphi^{(\alpha)}}{\partial x^k} + \sum_{\beta=1}^{p} \varphi^{(\beta)} \lambda_k{}^{(\beta\alpha)} = 0. \tag{7.4}$$

In consequence of (7.3) this system of equations is completely integrable, and hence there exists a set of φ's which by means of (7.1) determine a system of g's which yield a Riemann geometry. Hence we have the theorem: *In order that the geometry of paths shall be a Riemann geometry it is sufficient that the* Γ*'s be such that the equations* (5.3) *be algebraically consistent, and that all of their solutions satisfy* (5.5).

RICCI'S PRINCIPAL DIRECTIONS FOR A RIEMANN SPACE AND THE EINSTEIN THEORY

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In 1904 Ricci (*Atti R. Ist. Veneto*, **62**, 1230) developed the idea of principal directions in a Riemann space of n-dimensions, and in doing so introduced the contracted curvature tensor, which is fundamental in the Einstein theory, and gave a geometrical interpretation to it. A space in which these principal directions are completely indeterminate may be thought of as possessing a homogeneous character. We derive Ricci's results by a slightly different method, and then show that the three types of space, chosen by Einstein in 1914, 1917 and 1919, as spaces free from matter are of this homogeneous character, and include all types of such spaces.

Consider a Riemann space V_n of n-dimensions with the linear element

$$ds^2 = g_{ij}\,dx^i\,dx^j \,(g_{ij} = g_{ji}). \tag{1}$$

The right-hand member represents the sum of terms as i and j take on the values $1, \ldots\ldots n$, in accordance with the usual convention in such formulas that any term represents a summation with respect to each letter which appears in it both as a subscript and a superscript.

Suppose that we have in V_n n orthogonal unit vectors and let λ_h^i $(i = 1, \ldots\ldots n)$ denote the contravariant components of the vector (h). Then we have

$$g_{ij}\lambda_h^i\lambda_k^j = \delta_{hk}, \tag{2}$$

where

$$\delta_{hk} = \begin{matrix} 1 \text{ for } h = k \\ 0 \text{ for } h \neq k. \end{matrix} \tag{3}$$

If we take the surface consisting of the geodesics tangent at a point P to the pencil of directions determined by the lines of two congruences (h) and (k) through P, the gaussian curvature of this surface at P is given by

$$r_{hk} = R_{pq,rs}\,\lambda_h^p\,\lambda_k^q\,\lambda_h^r\,\lambda_k^s, \tag{4}$$

where $R_{pq,rs}$ is the Riemann tensor of the first kind. By definition r_{hk} is the Riemann curvature of V_n at P for the directions (h) and (k) (cf. Bianchi, **1**, 342).

Since the n vectors are mutually orthogonal, we have

$$\sum_k \lambda_h^q\lambda_k^s = g^{qs}, \tag{5}$$

where g^{qs} is the cofactor of g_{qs} in the determinant of the g's divided by the determinant. Hence from (4) we have

$$\sum_k r_{hk} = - R_{pr}\lambda_h^p\lambda_h^r, \tag{6}$$

where

$$R_{pr} = - g^{qs}R_{pq,rs}, \tag{7}$$

and consequently is the contracted curvature tensor. From (4) it follows that $r_{hh}=o$, and therefore

$$\rho_h = \sum_k r_{hk} = - R_{pr}\lambda_h^p\lambda_h^r \tag{8}$$

is the sum of the Riemann curvatures determined by (h) and each of $n-1$ directions orthogonal to (h). Ricci calls ρ_h the *mean curvature* of V_n for the direction (h) at the point. Thus Ricci not only obtained the fundamental contracted tensor in 1904, but gave a geometrical interpretation of it.

In general as the vector (h) is changed the value of ρ_h varies. Since the components λ_h^p are bound by the equations $g_{pr}\lambda_h^p\lambda_h^r = 1$ in order to find the directions giving the maximum and minimum values of ρ_h, we equate to zero the derivatives with respect to λ_h^r $(r=1,\ldots\ldots n)$ of

$$\rho_h = - \frac{R_{pr}\lambda_h^p\lambda_h^r}{g_{pr}\lambda_h^p\lambda_h^r}. \tag{9}$$

This gives

$$(R_{pr} + \rho_h g_{pr})\lambda_h^p = 0. \tag{10}$$

Hence the maximum and minimum values of ρ_h are the roots of the equation

$$\left| R_{pr} + \rho g_{pr} \right| = 0, \tag{11}$$

and the direction for each ρ is given by the corresponding n equations (10) for $r=1,\ldots\ldots n$. Following Ricci we call these n directions the *principal directions* of the V_n. It is readily shown that if the roots of (11) are distinct, the n corresponding directions are mutually orthogonal.

If $\lambda_{h|p}$ denote the covariant components of (h), and we multiply (10) by $\lambda_{h|p}$ and sum for h, we have

$$R_{pr} = - \sum_h \rho_h\lambda_{h|p}\lambda_{h|r},$$

which is the form given by Ricci as characteristic of principal directions.

In order that the principal directions be completely indeterminate at every point, it is necessary that the coefficients of the λ's in (10) be zero; that is

$$R_{pr} = \varphi g_{pr}, \tag{12}$$

where φ is a scalar. When this is satisfied, we have from (9) that ρ_h is the same for all directions. Consequently the space may be thought of as homogeneous, and (12) is the necessary and sufficient condition for such homogeneity.

From (12) we have

$$R = g^{\rho\tau}R_{\rho\tau} = n\varphi,$$

and (12) becomes

$$R_{\rho\tau} = \frac{1}{n} g_{\rho\tau}R. \qquad (13)$$

The original Einstein equations (1914) for space free from matter are those for which $\varphi = 0$ in (12); in 1917 (*Sitz. Pr. Ak. Wiss.*, Feb. 8), those for which $\varphi = \text{const.}$; and in 1919 (*Ibid.*, Apr. 10), the general case (13) of a homogeneous space from the above point of view.

From (8), (9) and (12) it follows that for any three mutually orthogonal directions in any 3-space, which is homogeneous,

$$r_{12} + r_{13} = r_{21} + r_{23} = r_{31} + r_{32} = -\varphi,$$

whence

$$r_{12} = r_{13} = r_{23} = -\frac{\varphi}{2}.$$

Thus the Riemann curvature at each point is the same for all directions, and by the theorem of Schur (*Math. Ann.*, **27**, 563) is constant. Consequently the first type of Einstein space is a generalization of euclidean 3-space, and his other two spaces of 3-space of constant curvature.

NOTE ON THE DEFINITION OF A LINEAL FUNCTIONAL

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A linear functional is usually defined as one that is distributive and continuous, but the term continuous functional has been used in at least two ways which are not equivalent. F. Riesz, Fréchet, G. C. Evans and others have defined a continuous functional as one which satisfies the equation

$$\lim_{n \to \infty} L(u_n(x)) = L(u(x)), \qquad (1)$$

when the sequence $u_1(x)$, $u_2(x)$, ... approaches $u(x)$ uniformly, while Levy[1] and W. L. Hart[2] have simply assumed that the sequence of u_n's converge in the mean. In Levy's paper the functional also depends on a parameter which has the same range as x, and $L(u_n(x),y)$ is only required to converge to $L(u(x),y)$ in the mean, but such a parameter will not be introduced here.

In what follows a distributive functional will be called linear when equation (1) is satisfied for uniformly convergent sequences of u's, and linear-m when they are only required to converge in the mean. If then L is to be linear it is necessary and sufficient that the equation

$$L(au_1 + bu_2) = aL(u_1) + bL(u_2) \qquad (2)$$

shall be satisfied, and that there be an M independent of u which satisfies the inequality

$$|L(u)| \leqq M . max|u|, \tag{3}$$

while if it is to be linear-m this inequality must be replaced by

$$|L(u)| \leqq M \sqrt{\int_a^b u^2(x)dx}. \tag{4}$$

F. Riesz has proved that every linear functional can be put into the Stieltjes form

$$L(u) = \int_a^b u(x)d\alpha(x), \tag{5}$$

where $\alpha(x)$ is independent of u and has finite variation.[3] Fréchet has reduced this to the form

$$L(u) = \sum_{n=1}^{\infty} A_n u(x_n) + \int_a^b u(x)\beta(x)dx + \int_a^b u(x)d\lambda(x), \tag{6}$$

where the A_n's are constants, the x_n's are the points where $\alpha(x)$ is discontinuous, $\beta(x)$ is the derivative of $\alpha(x)$ where the derivative exists, and $\lambda(x)$ is continuous, and has its derivative equal to zero excepting on a set of measure zero.[4] The principal object of the present note is to prove that when L is linear-m equation (6) becomes simply

$$L(u) = \int_a^b u(x)\beta(x)dx. \tag{7}$$

The class $[u(x)]$ will include all bounded, real-valued functions defined on (a, b), which are integrable with respect to a function of finite variation by Young's method of monotone sequences, beginning with the set of continuous functions.[5]

In the proof of equation (5) it was only assumed that $L(u)$ is defined for continuous u's, and to make the theorem apply to the larger class, L must always be defined in such a way that whenever a monotone sequence $\{u_n(x)\}$ approaches a discontinuous $v(x)$, $L(u_n)$ will approach $L(u)$. When this is done equation (6) will also be satisfied for the larger domain $[u(x)]$, since the limiting processes extending the definition of the Stieltjes integral (5) to the domain $[u(x)]$ will make each term of equation (6) approach the proper value. On the other hand if such a monotone sequence approaches $u(x)$, the equation

$$\lim_{n \to \infty} \int_a^b (u_n - u)^2 dx = 0$$

must be satisfied.[6] Then if L is linear-m inequality (4) implies that $L(u_n - u)$ will approach zero, and $L(u_n)$ must approach $L(u)$.

Since a uniformly convergent sequence must converge in the mean, a linear-m functional must also be linear.

If $L(u)$ is linear-m, and $u(x)$ is defined as identically zero excepting at x_1 where it is equal to unity, equation (6) becomes $L(u)=A_1$, and inequality (4) implies that $A_1=0$. Similarly $A_2=A_3=\ldots\ldots=0$. In other words $\alpha(x)$ must be continuous.

Since $\alpha(x)$ also has finite variation, it can be put into the form $\alpha(x)=\alpha_1(x)-\alpha_2(x)$, where α_1 and α_2 are continuous, have finite variation, and are monotone increasing. The derivatives of α_1 and α_2 will be called β_1 and β_2. A set E of measure zero will contain all points where either β fails to exist. Since no derivative number of a monotone increasing function can be negative, the functions $\lambda_i(x)$, defined by the equations

$$\lambda_i(x)=\alpha_i(x)-\int_a^x \beta_i(x)dx, \qquad (i=1, 2) \tag{8}$$

must be monotone increasing,[7] and their derivatives will vanish excepting on E. If a $k_1>0$ is now given, there must be a sequence of non-overlapping open intervals, $B_1=\sum_{n=1}^{\infty} I_n$ containing each point of E as an interior point of some I_n, such that the measure of B_1 is less than k_1. Then the variation of λ_i on B_1 is equal to its variation on (a, b),[8] which is $\lambda_i(b)-\lambda_i(a)$. The lower semicontinuous functions $u_1(x)$, $u_2(x)$,..... will now be defined by the equations

$$u_n(x)=1 \text{ on the interior of the intervals } I_1, I_2, \ldots\ldots I_n,$$
$$u_n(x)=0 \text{ for all other values of } x,$$

and consequently

$$\int_a^b u_n(x)d\lambda_i(x)=\text{Variation of } \lambda_i \text{ on } \sum_{m=1}^{n} I_m, \ (i=1, 2; n=1, 2, \ldots).$$

The limit $v_1(x)$ of this monotone sequence of u's, which vanishes excepting on B_1, must satisfy the equations

$$\int_a^b v_i(x)d\lambda_i(x)=\lambda_i(b)-\lambda_i(a). \qquad (i=1, 2)$$

If a sequence $k_1>k_2>\ldots\ldots\longrightarrow 0$ is chosen, beginning with the above k_1, the sequences of intervals B_2, B_3,..... can be chosen in such a way that each contains E, every point of each is a point of the preceding, and the measure of B_j is less that k_j. Then the sequence $v_2(x)$, $v_3(x)$,....., determined as $v_1(x)$ was, will be monotone decreasing, and its limit $v(x)$ will vanish excepting on a set of measure zero, and satisfy the equations

$$\int_a^b v(x)d\lambda_i(x)=\lambda_i(b)-\lambda_i(a). \qquad (i=1, 2) \tag{9}$$

Since $v(x)$ vanishes excepting on a set of measure zero, the equations

$$\int_a^b v(x)\beta_i(x)dx=0, \qquad (i=1, 2)$$

must be satisfied, and inequality (4) implies that $L(v) = 0$. But since $L(u)$ must satisfy equation (6) which is now equivalent to

$$L(u) = \int_a^b u(x)(\beta_1(x) - \beta_2(x))dx + \int_a^b u(x)d(\lambda_1(x) - \lambda_2(x)), \qquad (10)$$

it is necessary that

$$\int_a^b v(x)d(\lambda_1(x) - \lambda_2(x)) = 0.$$

Then equation (9) implies that $\lambda_1(b) - \lambda_2(b) = \lambda_1(a) - \lambda_2(a)$.

If in the above proof the functions $u_n(x)$, $v_j(x)$, and $v(x)$ had been defined as they were on the interval (a, y), where y is an arbitrary point on (a, b), and as identically zero on the rest of (a, b), the same argument would prove that $\lambda_1(y) - \lambda_2(y) = \lambda_1(a) - \lambda_2(a)$. That is, $\lambda_1 - \lambda_2$ is a constant, and equation (10) is equivalent to equation (7), with $\beta = \beta_1 - \beta_2$. This completes the proof of the theorem.

If L also depends on a parameter, y, and if instead of assuming that equation (1) is satisfied for every value of y, it is assumed that $L(u_n(x),y)$ approaches $L(u(x),y)$ in the mean, the theorem does not apply. For instance the functional

$$L(u(x),y) = u(y)$$

satisfies this condition, but cannot be represented by an integral analogous to (7).

[1] Levy, *Bul. Soc. Math. France*, **48**, 1920 (20).

[2] Hart, *New York, Bul. Amer. Math. Soc.*, **27**, 1921 (308).

[3] F. Riesz, *Ann. Sci. Ec. Norm., Paris* (Ser. 3), **31**, 1914 (9–14).

[4] Fréchet, *New York, Trans. Amer. Math. Soc.*, **15**, 1914 (152), or Evans, *Cambridge (Mass.), Colloquium Lectures* (60).

[5] Young, *Proc. London Math. Soc.*, **13**, 1914 (137), or Daniell, *Princeton, Ann. Math.*, **19**, 1917 (288–93).

[6] Bliss, *New York, Bul. Amer. Math. Soc.*, **24**, 1917 (24, corollary).

[7] *Ibid.* (38, Lemma 8).

[8] *Ibid.* (36–40, Theorems, 18 and 19).

SKIN TRANSPLANTATION IN FROG TADPOLES

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1. The experimental inhibition of vision by means of opaque grafts over the eyes of frog tadpoles (from 20 to 100 mm. in length) should contribute evidence as to any regulatory interaction between the graft and the eye, tending to restore the function of the eye. For this purpose 202 operations were performed upon two species of Rana, catesbeiana and clamatans, which had been collected from three widely separated sources.

The first grafts consisted of tail skin placed over the eye. Sixty-six per cent of these showed an adjustment whereby a small part of the graft was absorbed in a manner which tended to restore vision. When back skin was used, no such absorption occurred. Skin from the tail or back, grafted on other parts of the body, persisted indefinitely. However, when tail skin was grafted over hemispheres of glass or celloidin with radii equal to the radius of the eyeball, absorption occurred. The process in these grafts over "artificial eyes" was like that over normal functional eyes. Back-skin grafts so placed were not absorbed. As a check experiment, to determine whether or not the presence of the foreign material caused the absorption, other operations were made in which thin plates of glass cut from the ordinary cover-slip were used instead of the hemispheres. Such grafts were not absorbed, proving that the foreign material was not the cause of absorption.

From a study of the transplants, it was concluded that the curvature of the eyeball and of the artificial eye is the cause of absorption of tail-skin grafts. The plastic tail skin yields to the tension produced by the curvature and adjusts itself. In the majority of cases, this adjustment by absorption of tissue incidentally restores vision. It always ceases as soon as the tension is relieved. When the graft is very thick or is unusually well attached to the host, no adjustment is possible. Nor is it possible in back-skin grafts, because of their more compact structure.

The proliferation of new tissue by the transplants was limited to the tail-skin grafts. In some cases miniature tail tips were formed, while in others irregular proliferation predominated. This latter type is called "amorphic regeneration." The original anterior end, as well as the posterior end, of the graft is able to produce a new notochord and nerve cord in the regenerated tissue. It was found that the absence of light hastens the proliferation period by about nine days, and slightly increases the rate of proliferation. "Dark" grafts regularly showed amorphic regeneration. Following the period of proliferation, all grafts entered a state of equilibrium. In none of the grafts taken from the back or the belly was proliferation observed.

The conclusion is reached that no functional regulation of skin grafts over the eyes occurs. The adjustment which does take place is purely mechanical and its relation to the visual function is quite incidental. The lack of correlative regulation is probably the result of the high state of differentiation and specificity attained by the eye and the skin.

2. When integument from the tail, belly, or back is transplanted to another region on the same animal (auto-transplant), it preserves its characteristic appearance and produces new tissue of its own kind indefinitely. An homoio-transplant (from another individual not closely related) preserves its integrity only temporarily, being ultimately replaced

by regenerated host tissue. From these facts it is concluded that the integument of frog tadpoles is locally specific, and self-differentiating even when transferred to a new soil on the same animal.

3. Auto- and homoio-transplants of white belly skin on the dark back regions always acquire melanophores. The process varies according to the source of the transplant. In auto-transplants there is no antagonistic reaction between the protoplasms of the graft and the host, and union is quickly established. Melanophores appear only after several weeks, sometimes months. They are accompanied by the appearance of an abundance of scattered melanin granules and irregular masses of pigment, which may readily be interpreted as due to the presence of "young" melanophores. In homoio-transplants, union is delayed by the action of the homoio-toxin. In an effort to cover the wound as soon as possible, the surrounding epidermal cells migrate rapidly over the wound, and over the graft as though it were a foreign body. Melanophores are carried along. Such epidermal pigmentation may occur within twenty-four hours. Subsequent increase in the number of epidermal melanophores and the appearance of dermal melanophores and xantholeucophores are caused by formation *in situ* as a result of the normal growth activity of the integument.

It may therefore be said that in auto-transplants the acquisition of melanophores is chiefly the result of formation of pigment from the epithelial cells *in situ*, while in homoio-transplants the pigmentation is chiefly the result of epidermal migration which carries along melanophores. It may be followed by formation *in situ*.

4. When the conjunctiva of frog tadpoles is extensively injured by scratching or pricking, the regenerated tissue is pigmented first by epidermal melanophores and later by dermal melanophores and xantholeucophores. Such pigmentation, which may obscure the eye and presumably impair vision, persists indefinitely. It is further proof that no regulatory action between the eye and the overlying skin exists in tadpoles over 20 millimeters in length. The method of appearance of the pigment throws further light on the question of epidermal wound healing. The extensive injury of the conjunctiva compels the surrounding skin to repair the wound. The epidermal cells migrate over it and carry along the melanophores. Subsequent increase of pigment results from mitotic multiplication of integumentary cells.

5. A series of experiments was performed to discover the stimuli causing expansion and contraction of the dermal melanophores. Briefly, it was found that expansion is caused by a low temperature (near 0° C.) independently of illumination; by darkness; by a 0.1% chloretone solution; by anoxemia and by a low metabolic rate coincident with a moribund state. Contraction of the dermal melanophores is caused by a high temperature (near 35° C.) independently of illumination; by light, and

by a return of normal environmental conditions after removal of the effects of chloretone and anoxemia. Recovery from a moribund state also is accompanied by contraction.

Either expansion or contraction usually requires about thirty-six hours for completion, although the reactions begin within twenty minutes after initiation of the stimulus. Oxygen deficiency brings about complete expansion in about one-half hour. It is probable that any stimulus which lowers the metabolic rate of the whole animal also causes expansion of the melanophores, and any stimulus causing an increase in the metabolic rate results in contraction of the melanophores.

The complete account of these investigations will appear shortly in the *Journal of Experimental Zoölogy*.